

**ESTIMATION OF REPRODUCTIVE AND DEMOGRAPHIC
PARAMETERS OF THE EASTERN SPINNER DOLPHIN
(*STENELLA LONGIROSTRIS ORIENTALIS*)
USING AERIAL PHOTOGRAMMETRY**

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ABSTRACT

We counted and measured individual eastern spinner dolphins on vertical aerial photographs taken between 1980 and 2000 to collect information on school and population structure independent of previous data collected from the purse seine fishery for yellowfin tuna. From the count data, animals swimming in a distinct formation were identified as calves. This estimate was compared across the time series spanned by the data (from 1980 to 2000), among schools of different species compositions, and among schools of different sizes. The proportion of calves in schools photographed in 1998 and 2000 was significantly lower than that for 1988, 1992, and 1993 ($P < .05$), although no trend could be detected across the entire time series. The proportion of calves in a school was not significantly related to the species composition (pure eastern spinner schools versus schools composed of spotted and spinner dolphins) or the number of spinner dolphins in a school. From measurement data, animals were assigned to calf, juvenile, or adult age class according to length. No trend in proportion of juvenile animals (from 147 to 164 cm) was detected over the study period (from 1987 to 2000). Some schools were found to contain a larger proportion of juvenile dolphins than expected by chance, but no predominantly juvenile schools were found like those reported in a similar analysis of striped dolphins. The length distribution of all animals measured from photographs collected between 1987 and 2000 was composed of 10.4% calves, 22.8% juveniles, and 66.8% adults. This second proportion calves estimate, obtained from measurement data, differs from the estimate obtained from count data. The estimated length at which an eastern spinner calf disassociates from its mother was 142.1 cm, roughly two years of age, much longer than the average estimated age at weaning for this stock. Back-calculation of birthdates from animals up to one year of age from photographic and kill specimen data from the fishery indicated that there is a difference in the distribution of birthdates between animals sampled from inshore and offshore regions of the stock's range.

INTRODUCTION

Since the 1950's, purse seine vessels fishing for yellowfin tuna in the eastern tropical Pacific (ETP) have utilized the association between tuna and certain dolphin species by encircling schools of dolphins in order to capture the tuna swimming beneath them (Perrin, 1969). High incidental rates of mortality of encircled dolphins led to a significant reduction in the abundance of several dolphin species and stocks, primarily from the *Stenella* genus (Wade, 1995). Three stocks of tropical dolphins have been particularly affected by the fishery: northeastern offshore spotted (*Stenella attenuata*), coastal spotted (*Stenella attenuata graffmani*) and eastern spinner (*Stenella longirostris orientalis*), and consequently have been listed as depleted under the U.S. Marine Mammal Protection Act. An estimated 1,459,353 eastern spinner dolphins have been killed in the purse seine fishery between 1959 and 1997 (Southwest Fisheries Science Center, 1999). By 1988, this stock was estimated to have declined to approximately 44% of its pre-exploitation abundance, prompting the determination of its depleted status (Wade, 1993). However, after the 1990s reported dolphin mortalities were substantially

reduced to a very low level relative to estimated population levels for those years (Southwest Fisheries Science Center, 1999).

In spite of the apparent decrease in mortality rates, concerns over the impact of repeated chase and encirclement of tropical dolphin stocks by this fishery led the U.S. Congress to include studies of chase and encirclement in the International Dolphin Conservation Program Act (Public Law 105-42), passed in 1997. This act required the National Marine Fisheries Service to conduct surveys of depleted dolphin stocks and to determine whether fishing operations might still be having an adverse impact on these populations. One item of specific concern was whether cows with calves might have some increased disadvantage of survival by repeated chase and capture in the purse seine net. Comparison of numbers of lactating females and calves in kill sets on spinner and spotted dolphins indicates that there were significantly fewer calves than lactating females present (Archer *et al.*, 2001). This reported calf deficit implies that there is some disruption of the cow/calf bond caused by the purse-seining process, which would contribute additional mortality to the population that had been previously imperceptible. The significance of this finding on the ability of dolphin populations to recover depends on several factors, including the length of time that a calf is dependent on its mother.

Several questions remain unanswered concerning the social and age structure of the eastern spinner dolphin. It has been reported that the spotted dolphin, often found associated with the eastern spinner in mixed-species schools, has a nonrandom pattern of age segregation among schools sampled. There is a reported dearth of immature spotted dolphins from a sample of animals killed in the ETP purse seine fishery (Barlow and Hohn, 1984), along with evidence that juvenile spotters segregate from other dolphins into separate schools (Hohn and Scott, 1983). In addition, Perryman and Lynn (1994) found that another dolphin species inhabiting the ETP, the striped dolphin (*Stenella coeruleoalba*), exhibits segregation into schools composed of predominantly juvenile animals. The Japanese population of the striped dolphin is also reported to segregate into distinct juvenile and adult schools (Kasuya *et al.*, 1974, Miyazaki and Nishiwaki, 1978). It is currently unknown whether eastern spinner dolphins in the ETP show a similar pattern of segregation by age.

For this study, we have systematically examined vertical aerial photographs of schools of eastern spinner dolphins. These images were collected by scientists at the Southwest Fisheries Science Center as part of an ongoing study of the structure and abundance of dolphin populations in the eastern tropical Pacific. From these photos, we analyzed aspects of the social structure, age structure, and behavior of a school in a relatively unbiased manner compared to the sampling of sets of animals killed in the fishery (Powers and Barlow, 1979). By counting proportions of animals swimming in distinct formations, we estimated the proportion of a school composed of cows and calves to obtain an index of calf production over time. We also measured the lengths of animals and the distances between spatially associated neighbors to produce length frequency distributions and to quantitatively describe different types of associations between individuals, respectively.

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer's comments can be found in Appendix A.

METHODS

Photograph collection

The dolphin counts and measurements presented in this report were derived from vertical aerial photographs of eastern spinner dolphins collected from ship-based and land-based cetacean surveys conducted by the National Marine Fisheries Service between 1980 and 2000. For data collected between 1987 and 2000, photographs were taken with military reconnaissance cameras which were mounted below the hull of a Hughes 500D helicopter. The helicopter was carried aboard the NOAA research vessel *David Starr Jordan* as part of a broad-scale survey undertaken to monitor trends in the abundance of dolphin stocks affected by the purse-seine fishery. Photographs were obtained from regions throughout the geographic range of the species. For data collected in 1980, photographs were taken from a fixed-wing AT11 aircraft as part of a cetacean survey conducted in collaboration with scientists from the Inter-American Tropical Tuna Commission along the Pacific coast of Mexico. Photographs from this year are from the coastal portion of the species' range and likely represent a more restricted subsample of animals from the entire population.

Two military reconnaissance cameras were used in both studies and were remotely operated from a control box contained in the passenger cabin. One camera was typically outfitted with a telephoto lens and high-resolution black and white film for the purpose of extracting length measurements from individual animals in a school. The other camera was typically outfitted with a wide-angle lens and color film for the purposes of counting as many animals as possible in a school and of identifying them to species and by swimming association type (as described in next section). A series of photographic passes was made over the dolphin school during which the cameras fired shots continuously. Each pass was reviewed in order to select for analysis the pass that contained the largest number of dolphins swimming parallel to and near the sea surface. Individual 11.4 cm x 11.4 cm frames taken from the highest quality pass were analyzed under a magnifying scope at a light table in the laboratory. A more complete description of the processes involved in collecting photographs and extracting data from them is described in Perryman and Lynn (1993, 1994).

Count data

Individual animals were counted from photographs of 74 schools composed entirely of eastern spinner dolphins or a combination of eastern spinner and offshore spotted dolphins. The spatial relationship between each focal animal and the nearest individual swimming next to it was noted. We defined two distinct types of swimming associations between nearest neighbors. These associations were quantified in the standard manner described below to obtain an estimate of proportion calves in each school.

The cow/calf swimming formation (Fig. 1) was characterized by two animals of unequal lengths (the smaller animal identified as the 'calf', the larger animal identified as the 'cow') swimming in tandem, with the calf: (1) oriented on the same horizontal plane

as the cow, with shortest distance between animals located near the dorsal fin region of the cow ("echelon" position) or, (2) oriented below the cow, with melon near the abdomen of the cow ("infant" position) (Gubbins *et al.*, 1999).

All other types of swimming associations were classified as non-cow/calf swimming formations. These were generally much looser associations between individuals and included various types of spatial arrangements between nearest neighbors, although echelon swimming was also common (Fig. 1). An individual who was classified as swimming in any formation other than cow/calf was counted as an adult. Individuals who appeared to be engaged in mating behavior or who were not part of a cohesive subgroup of the school were not considered for calculation of mean nearest neighbor distance between non-cow/calf pairs.

Dolphin pairs which were not clearly visible in the images and for which we could not determine with certainty the presence or absence of a calf were excluded from our counts. Lone animals which were not engaged in a distinct swimming association with another dolphin were assigned to adult or calf categories based on their length. A dolphin which was substantially smaller than the adults swimming near it was classified as a lone calf, although this was an extremely rare occurrence.

Proportion calves

To investigate possible patterns in the relative number of calves and the species makeup of a school, we performed a univariate analysis of variance (ANOVA) to test for differences in the mean proportion spinner calves counted among three types of schools: mixed-species schools of offshore spotter and eastern spinner dolphins containing a majority of spinners; mixed-species schools of offshore spotter and eastern spinner dolphins containing a majority of spotters; and pure eastern spinner schools. We then combined both types of mixed-species schools into one category and compared the mean proportion calves between pure and mixed schools via an unpaired t-test. A correlation Z-test was used to determine if a significant relationship existed between proportion calves and the total number of spinners counted in a school.

To determine if a trend in the proportion of calves was evident among the years sampled, we visually inspected a scatterplot of proportion calves versus year. To reduce the variation in the proportion of calves among schools sampled within the same year, we pooled these schools together to obtain one estimate for each year. We then examined this pooled estimate of proportion calves with respect to year to determine if it was appropriate to apply a linear model to detect a trend in proportion calves over year.

Because the proportion calves among schools within the same year was highly variable, the power to detect a trend in proportion calves across all years was low. To increase the power of detecting a trend, we pooled all schools within each year and performed a non-linear regression on this reduced dataset.

As an alternative approach to the detection of a trend across the entire time series, we performed two tests to investigate possible differences in the pooled estimate of the proportion calves among individual years. First, we performed a chi-square test to determine if the proportion of calves was independent of the year in which it was sampled. Second, we computed binomially distributed 95% confidence intervals around each annual point and compared the patterns of overlap in values among years.

Measurement data

Individual animals were measured from 29 schools, 26 of which were a subset of the count data mentioned above. Only those individuals who were swimming parallel to the sea surface and close enough to the surface so that both the tip of the rostrum and straight edge of the flukes were visible were selected for measurement. Measurements were made by capturing the original black and white negative image in digital format onto a large computer monitor using a SPOT digital camera system. Body length for each dolphin was determined by measuring the distance from the tip of the rostrum to the trailing edge of the tail flukes using the Image Pro Plus software package (by Media Cybernetics). We followed the procedure outlined in Perryman and Westlake (1998) to correct for possible biases in length measurements due to scale error and to convert from photographic lengths to real lengths.

School structure

We stratified the individual length measurements into the three types of schools described above, and compared the mean length of individuals among the three school types. Because none of the three length distributions were normally distributed, we performed a non-parametric analysis of variance of ranks test (Kruskal-Wallis) to test the hypothesis that the length measurements do not differ with respect to school composition.

We created age cohort-stratified length distributions for each school containing greater than seven animals measured by dividing individual length samples into three length categories which we labeled calf, juvenile and adult. For this analysis, we defined calves as animals less than or equal to 142.1 cm, the length at which there was an estimated 50% probability that an eastern spinner calf will be disassociated from its mother (from 'Length at independence' analysis, below). The maximum length for juveniles was defined as 164 cm, the average length at attainment of sexual maturity for female eastern spinner dolphins, as defined in Perrin *et al.* (1977) and Perrin & Reilly (1984).

A chi-square analysis was chosen to test the assumption that the number of juvenile animals and adult animals in the schools measured were independent of school. Animals labeled as calves were excluded from the analysis. The individual contribution of each of the schools to the overall chi-square statistic was compared to determine whether there were schools which contained a disproportionate number of juveniles.

To determine if a temporal trend in the proportion juveniles was apparent in the schools sampled, we visually inspected a scatterplot of proportion juveniles versus year. To reduce the variation in the proportion of juveniles among schools sampled within the same year, we then pooled these schools together. We produced a new scatterplot of proportion calves using this data and examined the pooled point estimates to determine if it was appropriate to apply a linear model to detect a trend in the proportion of juveniles with respect to year.

A simple linear regression was used to determine if there was a significant relationship between the proportion of juveniles and year. A power analysis was then performed to determine the ability of the linear regression to detect a temporal trend in proportion calves. An updated version of the TRENDS software program described in Gerrodette (1993) was employed for the power analysis.

Two alternative methods were employed to investigate possible differences among individual years sampled. A chi-square test was performed using the pooled data to determine if the proportion juveniles was independent of year. In addition, binomially distributed 95% confidence intervals were computed around the pooled proportion juveniles to test for significant differences among years.

Next, all eastern spinner length data derived from aerial photographs was combined to construct a length frequency distribution. This distribution was divided into three age cohorts (calf, juvenile, and adult) by the method described above to obtain the overall proportions of each of the three age categories given by the data collected.

Length at independence

We compiled measurement and count data to produce a dataset containing length of each animal and a binary variable indicating association or lack of association with a cow (as defined by the presence or absence of a cow/calf swimming configuration). The probability of association with a cow was modeled as a function of length of animal using a logistic regression. We maximized a log-likelihood function to fit the data to each of three possible logistic models, of the general form $\ln(y/1-y) = e^{(\$0+\$1x+\$2x^2)}$, to estimate the probability of association at a given length. We tested three models: the full model, with three non-zero \$ coefficients, and two models with \$1 or \$2 set to zero. We compared the calculated Akaike's Information Criterion (AIC) values (Burnham and Anderson, 1998) for the three possible models and selected the model with the lowest value. The length at which there was a 50% probability that an animal was associated with a cow was an indicator of estimated length at independence for eastern spinner dolphin calves; we called this the length at disassociation. Confidence intervals were computed by generating a bootstrapped distribution of 1000 estimated lengths at disassociation and then reporting the values located in the 5th and 95th percentiles of the distribution.

Timing of reproduction

To detect possible seasonal patterns in reproduction, we calculated birthdates of dolphins from photographic measurement data (from 1987-2000) and from individuals killed during tuna purse-seining operations and collected from NMFS scientific observers between 1968 and 1992 (n=725) (Susan Chivers, pers. comm., SWFSC unpub. data). From this combined dataset, we constructed a frequency distribution of birthdates for yearlings. Birthdates were back-projected from individuals' lengths and the date at which they were sampled. The postnatal growth rates reported in Perrin *et al.* (1977) were used to calculate birthdates only for animals defined as less than or equal to one year of age (134.0 cm), because growth is rapid relative to individual variation in growth rate for these young animals (Barlow, 1984).

Perrin *et al.* (1977) noted different peaks between the length frequency distributions of fishery specimens collected in inshore and offshore regions of the study area, and postulated this could be indicative of a geographic difference in the timing of reproduction. Barlow (1984) tested and confirmed this observation by drawing a line roughly parallel to the coastline and statistically comparing the birthdate distributions of animals from the two strata. We stratified the data in the same onshore/offshore pattern to produce distinct onshore and offshore regions (Fig. 2). We performed a two-sample Kolmogorov goodness of fit test as discussed by Batschelet (1965) and modified for

circular distributions by Kuiper (1960) to compare the distribution of birthdates between these two samples. We also performed a one-sample Kolmogorov test on each stratified birthdate distribution against a uniform distribution to detect the existence of temporally non-uniform breeding among animals from a similar geographic area.

With the exception of the maximum likelihood analysis, for which a program was written using Fortran code, and both the Kolmogorov test for circular distributions and the binomial confidence intervals for proportion calves and proportion juveniles which were done by hand, all statistical tests presented in this paper were performed with the StatView software package (SAS Institute Inc.). All tests described in this paper were considered significant for calculated P values < 0.05 , unless otherwise noted.

RESULTS

Sample size

A total of 8442 eastern spinner dolphins were counted from 74 schools (Table 1). We measured a total of 1476 dolphins from 29 schools, 26 of which were schools from the count dataset (Table 2). Three of the schools measured were not counted to obtain an estimate of proportion calves.

Cow/calf swimming association

The mean shortest distance between animals determined to be swimming in cow/calf formation was 14.31 cm ($n = 30$, $sd = 9.12$). The mean shortest distance between animals determined to be swimming in a formation other than cow/calf was 164.73 cm ($n = 37$, $sd = 105.66$), much greater and with a wider spread of distances than that for cow/calf pairs.

Proportion calves

The results of an ANOVA test found that there was no statistically significant difference among the three mean values of proportion calves for schools with different species compositions ($P = .8515$, $f = .161$). Pure eastern spinner schools had the highest proportion of spinner calves of the three types of school categories defined (mean = .071, $SE = .009$, $n = 24$), followed by majority spotter mixed-species schools (mean = .068, $SE = .018$, $n = 19$), then majority spinner mixed-species schools (mean = .063, $SE = .006$, $n = 30$). Proportion calves was normally distributed (one-sample K-S test, $P = .9411$). When we pooled majority spinner and majority spotter mixed-species schools into one 'mixed species' category, the proportion of spinner calves in pure schools was higher than in mixed schools (mean = .067, $SE = .008$, $n = 50$), although not significantly different (Student's unpaired t-test, $P = .730$). In addition, no statistically significant linear relationship was found between the proportion of eastern spinner calves and the total number of spinner dolphins counted in a school (correlation Z-test, $Z = -1.229$, $P = .219$; Fig. 3).

We combined eastern spinner schools of the three species compositions and found no significant linear relationship between the proportion of eastern spinner calves and year of sample (linear regression, $R^2 = .001$, $P = .768$, $n = 74$). Similarly, a linear trend

in proportion calves could not be discerned when schools sampled in the same year were pooled (linear regression, $R^2 = .028$, $P = .692$, $n = 9$). Rather than increasing or decreasing in a linear manner over the time series, the pooled proportion of calves was approximately curvilinear, with maximum values at the 1992/1993 points and minimum values at the 1980 and 1998/2000 points (Fig. 4). Removing the proportion calves estimate from 1980, the year for which schools were sampled in a different manner and in a more restricted geographic range, did not significantly change either the overall appearance of the data over the time series or the results of the regression analyses.

The results of the chi-square test performed on the data pooled within years indicated that the proportion of calves are significantly different among the years sampled. The analysis of post hoc chi-square contributions from each year showed that the proportion of calves in 1988, 1992 and 1993 were significantly higher than expected and the proportion of calves in 2000 was significantly lower than expected.

We compared the 95% confidence intervals around the pooled estimate for each year using the binomial distribution and found that the proportion calves in schools photographed in 1998 and 2000 is significantly lower than those from 1988, 1992 and 1993 (Fig. 5). Therefore, a significant decline in proportion calves was detected between data collected during the abundance survey conducted in the early 1990s and that collected from the most recent survey completed in 2000.

School structure

The Kruskal-Wallis test indicated that the length distributions from schools of the three species composition types were not significantly different ($P = .7213$; Fig. 6), therefore the species composition does not appear to be related to the length structure of the eastern spinner component of a school.

Visual inspection of a scatterplot of the proportion of juvenile animals in each school versus year in which the schools was sampled concluded that there was no apparent linear trend in the proportion of juvenile animals over time.

We performed a chi-square test to compare the ratio of the number of juvenile animals to adult animals among individual schools. We included 28 schools from which we divided length frequency distributions into juvenile and adult length categories (Fig. 7). The calculated chi-square value was found to be highly significant ($P < .0001$), suggesting that the ratio of juvenile animals to adult animals in a school is not randomly distributed among the schools measured. From post hoc analyses we concluded that four of these schools contained significantly more juvenile animals than expected by chance if the number of juveniles was independent of school, and two schools contained significantly fewer juveniles than expected by chance ($P < .05$). However, none of the schools examined exhibited the extent of segregation by age class as reported for striped dolphins in Perryman and Lynn (1994). We further examined the relative geographic positions and species compositions of the six eastern spinner schools containing a significantly disproportionate amount of juvenile animals and found no apparent pattern in the distribution of either of these characteristics. However, all of these schools were sampled in the years 1987, 1988, and 1989; therefore, the most extreme values of proportions of juvenile animals occur in the earliest three years of the time series sampled.

Visual inspection of a bivariate scatterplot of proportion juveniles in each school sampled and year showed that, although there appeared to be a slight downward pattern in the proportion juveniles over time, no linear relationship was apparent between the proportion juveniles and year of sample. A linear regression on schools pooled within the same year did not detect a linear trend in proportion of juvenile animals ($R^2 = .28$, $P = .19$, $n = 7$; Fig. 8). However, the power to detect a linear decrease in the proportion juveniles was low for this analysis; the minimum overall decrease in proportion juveniles which could be detected with 90% certainty was 87%.

The 95% confidence intervals around these points indicate that the proportion juveniles in 1987 is significantly higher than the proportion of juveniles in 2000 (Fig. 9). However, interpretation of this difference is made difficult by the fact that the estimate for 1987 was derived from measurements taken from a single school.

When we constructed a length frequency distribution from all photographic data collected and stratified it into the above-mentioned age classes, 10.4% of the animals were classified as calves, 22.8% as juveniles, and 66.8% as adults (Fig. 10).

Length at independence

The length at disassociation estimated from the probability function was determined to be 142.1 cm (Fig. 11). The 90% confidence intervals around this estimate were 140.046-143.628 cm ($n = 1199$). This estimate corresponds to an age at independence of approximately two years (Perrin *et al.*, 1977) for eastern spinner calves.

Timing of reproduction

The cumulative birthdate distributions for designated inshore and offshore groupings of the combined photographic and kill specimen length data were found to be statistically different by the two sample Kolmogorov's test ($P < 0.01$). There appears to be a relatively greater proportion of births earlier in the year among samples in the offshore region than among samples in the inshore region. While one distinct peak exists in both regions, the peak in calving occurs earlier in the year in the offshore sample (Fig. 12). This pattern is similar to the one observed in Barlow (1984), suggesting that some synchrony in calving exists for animals in different geographic regions.

DISCUSSION

From our examination of aerial photographs of eastern spinner schools, no relationship between the proportion of calves in a school and the size and species composition of the school was detected. Although a linear trend in the proportion of calves could not be apparent over the entire time series spanned by the data, we did find a significantly lower proportion of calves in schools sampled during the most recent abundance survey (in 1998 and 2000) compared to those sampled during the previous survey undertaken in the early 1990s.

Similarly, no significant linear trend in proportion juveniles (identified based on their length) over the time period from 1987 to 2000 was detected. The proportion of juvenile animals in 2000 was found to be significantly lower than the proportion of

juveniles in 1987, although it should be noted that the estimate for the latter year is based on measurements from one school.

The estimated proportion of calf and juvenile age categories is highly variable among schools both within and between the years sampled. This variability could be a reflection of the actual variable nature of the age structure among different schools, or could be due to biases present within the process of counting and/or measuring of individual dolphins. There are several factors which confounded our ability to determine the swimming configuration of every animal photographed from a school, and which likely resulted in biases in the absolute counts of calves and non-calves from each school.

It is likely that animals swimming deeper in the water and/or underneath other animals were not visible enough to be classified into cow/calf or non-cow/calf formation. In particular, calves swimming underneath the mother in infant position may have not been detected, possibly resulting in a negative bias to our estimate of the proportion of calves in a school. However, this negative bias may be dampened by the fact that calf swim behavior may make them easier to identify than older animals; the calves which we were able to identify and count were swimming higher in the water column and appeared more visible than other dolphins. In fact, while the average proportion of animals counted which were calves was 5.8%, the average proportion of animals measured which were calves was over twice that, 12.3%. This discrepancy suggests that of the animals counted, calves are more suitable for measuring because they are relatively more visible than other dolphins. As a result, the proportion of calves estimated by the measurement data could potentially have a positive bias. In addition, many more animals were counted than measured, indicating that the count data is a more reliable estimate of the proportion of calves.

Conditions such as glare from the sun, the presence of tightly-packed dolphin schools, and water surface disturbances caused by wind, swell and moving dolphins resulted in approximately 0%-70% of the school photographed left uncounted. It is uncertain if these factors disproportionately affect our ability to count dolphins swimming in cow/calf formation relative to those swimming in an alternate formation. So although it is likely that the subsample of animals counted in a school is a biased estimate of the *counts* of calves and non-calves, it is unknown if this subsample is a biased estimate of the *proportion* of calves in a school. It should be noted, however, that there was no significant difference in the estimated proportion of calves among schools grouped according to the percent of animals in the photograph which were uncounted. Regardless of the true nature of the bias, in the tests of proportion calves we assume that this bias is consistent among all the schools sampled.

In addition to possible biases in the reported proportion of a school composed of calves, there are likely other factors contributing to the variability in calf proportions across schools and time. It is improbable that the processes affecting the age structure and abundance levels of this population over the twenty-year period spanned by this study would be operating at a constant level. Demographic and environmental stochasticity, along with varying levels of fishery-related mortality, would cause fluctuations in age class-specific mortality rates. Similarly, this variability over the large range and long time span encompassed by the study could also contribute to the apparent differences in age structure among individual schools sampled. However, no relationship was found between the offshore distance of a school and the proportion of the school

comprised of calves; in this regard, the sample does not appear to be biased with respect to geographic location of sample. Further investigation should be conducted to determine if the proportion of calves varies with certain oceanographic factors associated with the position of the sample.

Although variability in age structure among schools exists, some schools were found to have a larger proportion of juvenile animals relative to adult animals than expected by chance. We did not, however, detect the pronounced pattern of segregation into schools by length that was reported from a similar study on striped dolphins (Perryman and Lynn, 1994). Striped dolphins were found to segregate into schools composed of a majority of juvenile animals. None of the eastern spinner schools examined in this paper were composed predominantly of juvenile animals; each of the schools sampled contained fewer juveniles than adults and calves combined. Therefore, it was concluded that juvenile eastern spinner dolphins were more uniformly dispersed among schools than juvenile striped dolphins. Although there does not appear to be a non-random pattern in the distribution of juvenile animals over schools in different regions, school size, and species composition, there does appear to be a temporal pattern. The four schools which contained significantly fewer juveniles and the two schools which contained significantly more juveniles were all sampled in the late 1980s. Apparently, the range of the proportion of juvenile animals was more extreme among the earliest years in the time series than in the later years.

The above limitations in interpreting the age structure of this population over large ranges of time and geographic location should be noted. However, with the addition of age class-specific mortality and fecundity rates, an age-structured population model could be fit to the length data to estimate the growth rate of the eastern spinner population.

If the eastern spinner dolphin population is well below the carrying capacity of its environment and the impact of the purse seine fishery on the population has been reduced to insignificant levels, the reproductive output of the population would be expected to increase. An increase in the proportion calves, and, later, juveniles, would be predicted to appear in the time series of the data collected. The absence of a detectable increase from our analyses in either the proportion of calf or juvenile age classes from the 1980s to the year 2000 could be at least a partial explanation for the population's failure to grow at its expected rate (Southwest Fisheries Science Center, 1999).

We found that the length of disassociation for eastern spinner calves was approximately 142 cm. Using the growth curve constructed in Perrin *et al.* (1977) it appears that on average eastern spinner dolphins begin swimming independently of their mothers at an age of approximately two years. This estimate of age at disassociation encompasses a much longer time period than the average age at weaning of 11 months reported in Perrin and Reilly (1984). Although it is unknown whether average age at disassociation can be interpreted as an average age at weaning, this estimate can at least serve as an indication of the age up to which an animal is still tightly associated with its mother, and therefore possibly more vulnerable to mortality if separated.

Most schools were photographed while the school was swimming rapidly or traveling, where associations between individuals, especially a cow and her calf, may be magnified with respect to spatial relationship. In another precocial species, bison, calves were shown to maintain increased close contact with their mothers during times of

herding (Green 1992), and the same phenomena was reported for reindeer (Espmark 1971). If the same pattern is exhibited in eastern spinner cow-calf pairs, then the distances measured between these pairs in rapid transit may be smaller than those maintained under normal circumstances. Similarly, cow-calf associations may become intensified or magnified in reaction to an event perceived as stressful, such as chase by a research vessel and/or aircraft. Mann, *et al* (1995) observed a dramatic increase in close contact and synchrony of movement between a wild bottlenose cow and calf during the calf's entanglement in a fishing line. This response may function as a means of protecting the calf during especially vulnerable occurrences and highlights the strength and significance of the cow-calf bond.

Gubbins *et al.* (1999) and Mann and Smutts (1999) report that both captive and wild bottlenose dolphin calves have an increased probability of being found in infant position (and a decreased probability of being in echelon position) as the calf grows during its first few years. This implies that younger calves are more likely to be found swimming in echelon position and older calves are more likely to be found swimming in infant position. The difficulty of detecting a calf in vertical aerial photographs when it is swimming underneath its mother in infant position may lead to a disproportionate amount of smaller animals sampled for the length at independence analysis, which could bias the resulting estimate downward. Therefore, the length of time (and age) which a calf may be dependent on its mother in some manner may be underestimated by this analysis. If separation of mother/calf pairs occurs during the purse-seining process, it may affect calves which are longer (i.e. older) than the length at disassociation estimated in this paper.

Lastly, the back-calculation of birthdates indicated that there was a geographic discrepancy in the timing of the birthing pulse for eastern spinners sampled in the offshore and inshore regions of their range. This pattern, similar to the one observed in Barlow (1984), suggests that some synchrony in calving exists for animals in different geographic regions. Although the reproductive peaks are diffuse, the presence of distinct peaks between the two samples implies that there may be some reproductive isolation between regions. If such reproductive barriers exist, then animals from different regions may function more as separate populations than is currently assumed, and should be managed accordingly.

LITERATURE CITED

ARCHER, F., T. GERRODETTE, A. DIZON, K. ABELLA AND S. SOUTHERN. 2001. Unobserved kill of nursing dolphin calves in a tuna purse-seine fishery. *Marine Mammal Science*, 17:540-554.

ANGLISS, R. P., C. H. RODERICK AND D. P. DEMASTER. 1995. Determination of the sample size necessary to detect changes in length frequency distributions from a recovering population of bowhead whales. *Reports of the International Whaling Commission* 45:331-334.

ANONYMOUS. 1999. Report to Congress on the initial finding, required under the Marine Mammal Protection Act of 1972 as amended by the International Dolphin Conservation Program Act of 1997. Prepared by the Southwest Fisheries Science Center, National Marine Fisheries Service, 25 March 1000. 54pp. [Available from: <http://swfsc.nmfs.noaa.gov/prd/congress/congress.htm>]

BARLOW, J. 1984. Reproductive seasonality in pelagic dolphins (*Stenella* spp.): implications for measuring rates. *Reports of the International Whaling Commission (Special Issue 6)*: 191-198.

BARLOW, J. AND A. HOHN. 1984. Interpreting spotted dolphin age distributions. Southwest Fisheries Center Technical Memorandum NOAA-TM-NMFS-SWFC-48. 22 pp. Available from Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038, U.S.A.

BATSCHELET, E. 1965. *Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms*. American Institute of Biological Science, Monograph, 57 pp.

BRODIE, P. F. 1969. Duration of lactation in Cetacea: An indicator of required learning? *The American Midland Naturalist* 82:312-314.

BURNHAM, K. P. AND D.R. ANDERSON. 1998. *Model Selection and Inference. A practical information-theoretic approach*. Springer-Verlag, New York, NY.

CHIVERS, S.J. AND D.P. DeMASTER. 1994. Evaluation of Biological Indices for Three Eastern Pacific Dolphin Species. *Journal of Wildlife Management* 58(3):470-478.

ESPMARK, Y. 1971. Mother-young relationship and ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). *Z. Tierpsychol.* 29:42-81.

GERRODETTE, T. 1993. TRENDS: Software for a power analysis of linear regression. *Wildlife Society Bulletin* 21:515-516

GREEN, W. C. H. 1992. The development of independence in bison: pre-weaning spatial relations between mothers and calves. *Animal Behavior* 43:759-773.

GUBBINS, C., B. MCCOWAN, S. K. LYNN, S. HOOPER AND D. REISS. 1999. Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science* 15(3):751-765.

HOHN, A. A. AND M. D. SCOTT. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Abstract, Fifth Biennial Conference on the Biology of Marine Mammals, Boston.

KASUYA, T., N. MIYAZAKI AND W.H. DOWBIN. 1974. Growth and reproduction of *Stenella attenuata* in the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.* 26:157-226.

KUIPER, N. H. 1960. Tests concerning random points on a circle. *Ned. Akad. Wetensch. Proc., Ser. A*, 63:38-47.

MANN, J., R. A. SMOLKER, AND B. B. SMUTS. 1995. Responses to calf entanglement in free-ranging bottlenose dolphins. *Marine Mammal Science* 11:100-106.

MANN, J., AND B. SMUTS. 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour* 136:529-566.

MIYAZAKI, N. AND M. NISHIWAKI. 1978. School structure of the striped dolphin off the Pacific coast of Japan. *Sci. Rep. Whales Res. Inst.*, 30:65-115

PERRIN, W. F. 1969. Using porpoise to catch tuna. *World Fishing* 18:42-45.

PERRIN, W. F., D. B. HOLTS AND R. B. MILLER. 1977. Growth and reproduction of the eastern spinner dolphin, a geographical form of *Stenella longirostris* in the eastern tropical Pacific. *Fishery Bulletin, U. S.* 75:725-50.

PERRIN, W. F. AND S. B. REILLY. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. *Reports of the International Whaling Commission (Special Issue 6)*: 417-430.

PERRYMAN, W. L. AND M. S. LYNN. 1993. Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. *Marine Mammal Science* 9:119-137.

PERRYMAN, W. L. AND M. S. LYNN. 1994. Examination of stock and school structure of striped dolphins (*Stenella coeruleoalba*) in the eastern Pacific from aerial photogrammetry. *Fishery Bulletin, U. S.* 92:122-131.

PERRYMAN, W. L. AND R. L. WESTLAKE. 1998. A new geographic form of the spinner dolphin, *Stenella longirostris*, detected with aerial photogrammetry. *Marine Mammal Science* 14:38-50.

POWERS, J. E. AND J. BARLOW. 1979. Biases in the tuna-net sampling of dolphins in the eastern tropical Pacific. Preliminary report for the Status of Porpoise Stocks workshop, Aug 27-31, 1979.

WADE, P. R. 1993. Estimation of historical population size of the eastern spinner dolphin (*Stenella longirostris orientalis*). Fishery Bulletin, U. S. 91:775-787.

WADE, P. R. 1995. Revised estimates of incidental kill of dolphins (Delphinidae) by the purse-seine tuna fishery in the eastern tropical Pacific, 1959-1972. Fishery Bulletin, U. S. 93:345-354.

Table 1. Summary of eastern spinner dolphins counted from aerial photographs.

	pure schools		mixed schools		total	
year	N _{schools}	N _{animals}	N _{schools}	N _{animals}	N _{schools}	N _{animals}
1980	0	0	14	1987	14	1987
1987	5	309	0	0	5	309
1988	5	1078	4	405	9	1483
1989	2	259	5	408	7	667
1990	3	194	6	180	9	374
1992	1	16	3	322	4	338
1993	3	301	3	292	6	593
1998	4	974	8	449	12	1423
2000	1	649	7	619	8	1268
totals:	24	3780	50	4662	74	8442

Table 2. Summary of eastern spinner dolphins measured from aerial photographs.

	pure schools		mixed schools		total	
year	N _{schools}	N _{animals}	N _{schools}	N _{animals}	N _{schools}	N _{animals}
1980	0	0	0	0	0	0
1987	0	0	1	34	1	34
1988	4	422	3	210	7	632
1989	2	111	2	75	4	186
1990	3	117	4	104	7	221
1992	0	0	2	42	2	42
1993	2	121	3	166	5	287
1998	0	0	0	0	0	0
2000	0	0	3	74	3	74
totals:	11	771	18	705	29	1476



Figure 1. Vertical aerial photograph of eastern spinner dolphin school typical of those analyzed in this paper. Pair of animals swimming in cow/calf formation are shown in upper right corner. All other animals in image are swimming in non cow/calf formations.

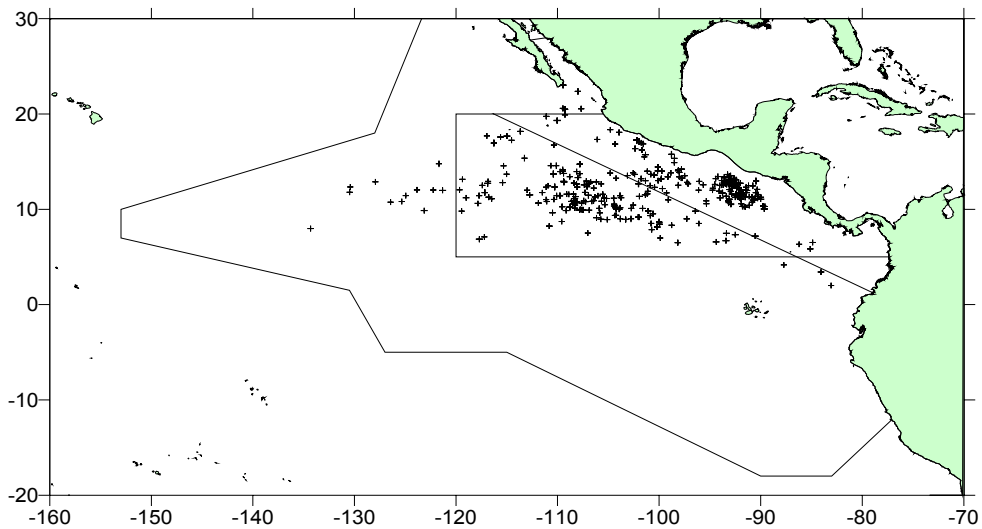


Figure 2. Geographic distribution of eastern spinner dolphin length measurements derived from aerial photographs and fishery kill data. Inshore and offshore strata are defined by diagonal line.

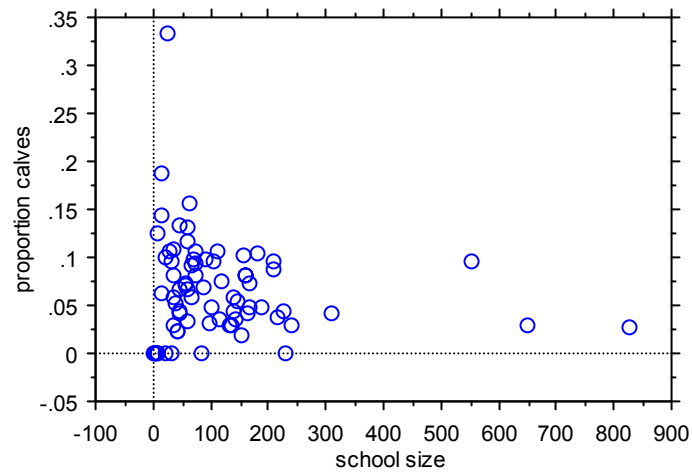


Figure 3. Proportion calves versus school size. School size is defined as the total number of spinner dolphins counted in a school.

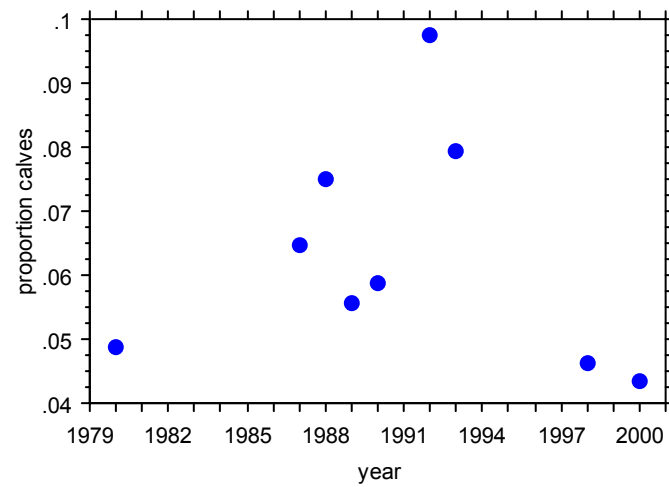


Figure 4. Proportion calves versus year in which school was photographed. Data from schools sampled in the same year are pooled.

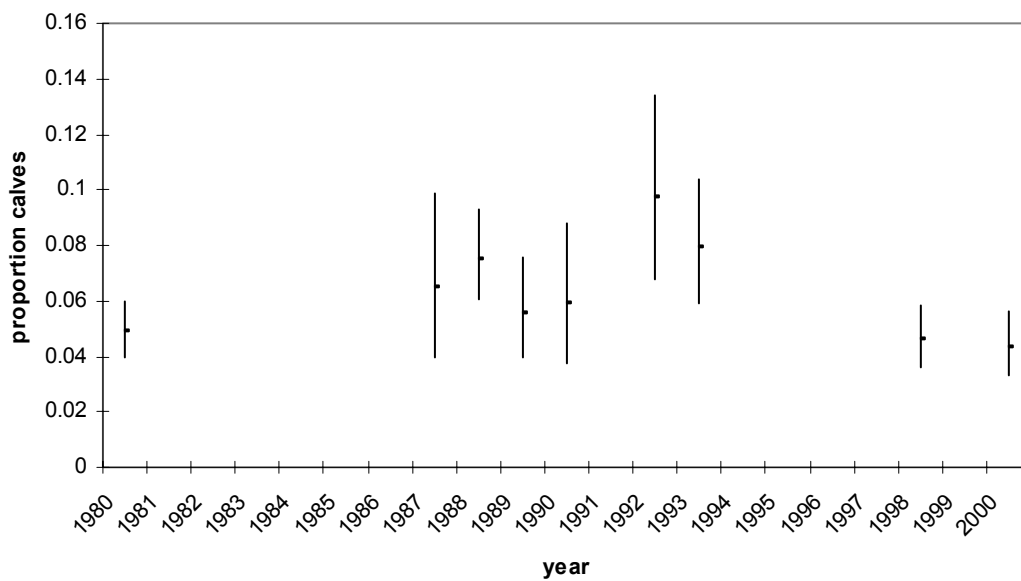


Figure 5. Proportion calves from data pooled within year with 95% binomial confidence intervals.

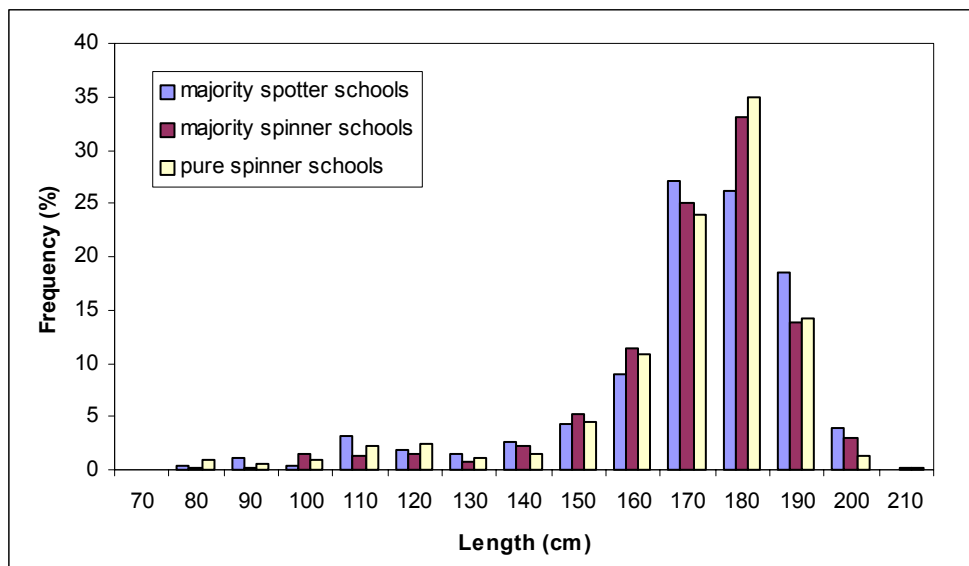


Figure 6. Distribution of body lengths of eastern spinner dolphins measured from photographs collected between 1987 and 2000. Mean length of all animals = 164.90 cm (sd = 21.10 cm).

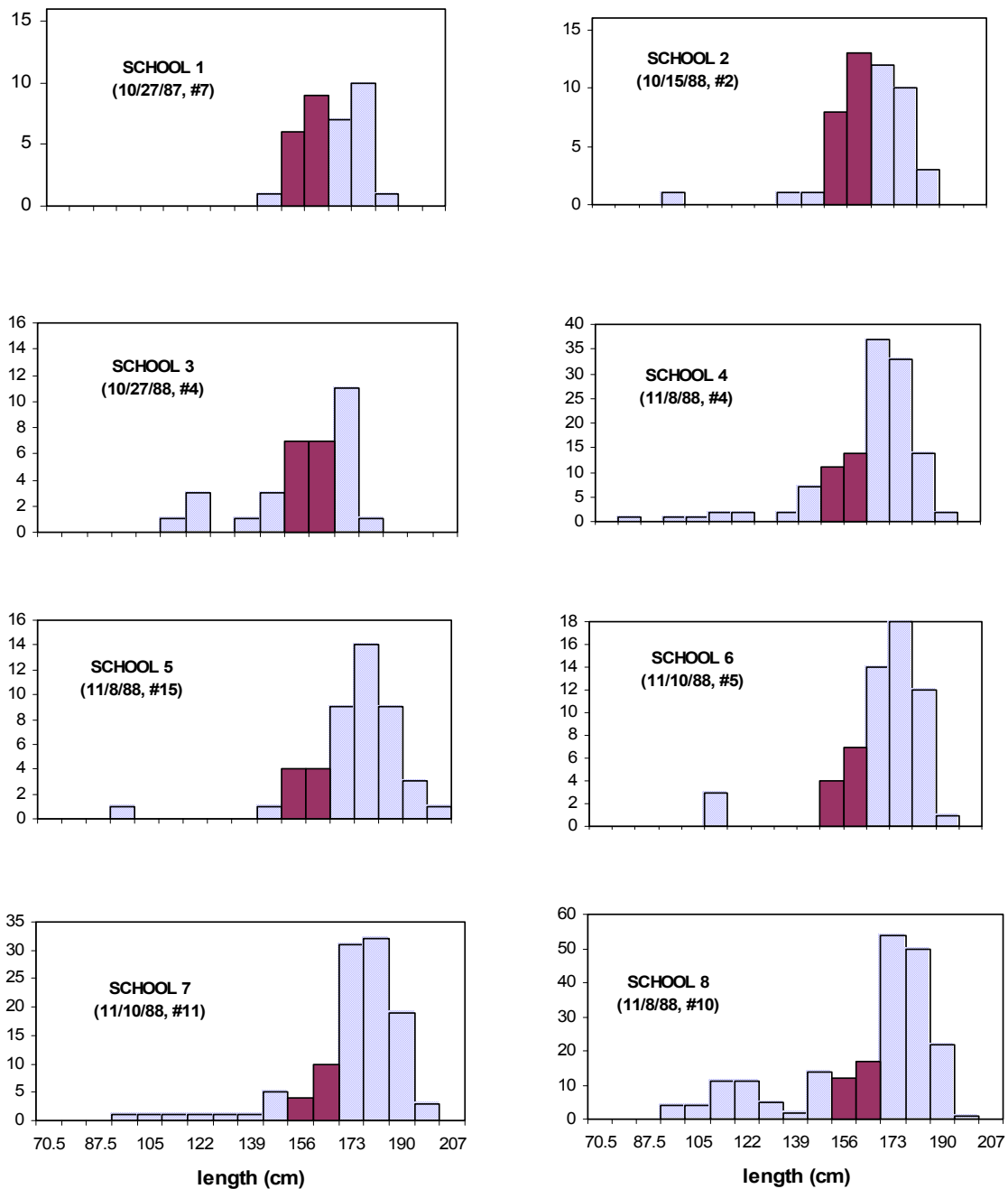


Figure 7. Length frequency distributions for each school examined in chi-square analysis comparing number juvenile animals among schools. Solid bars indicate lengths of individuals that were included in juvenile category. Schools 13, 14, 16, 20, 21, 26, and 28 were excluded from analysis due to low expected cell frequencies. Date and sighting number from SWFSC abundance survey are in parentheses.

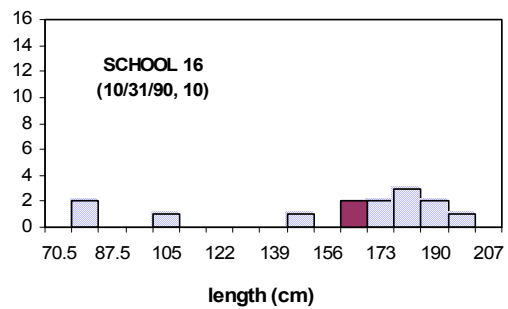
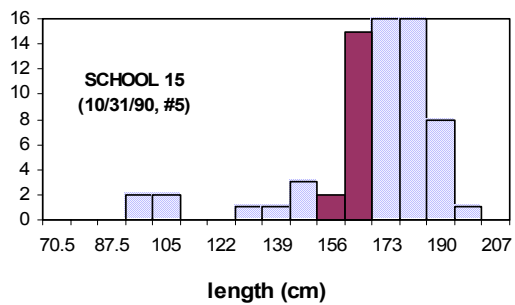
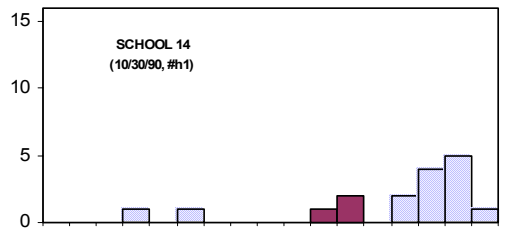
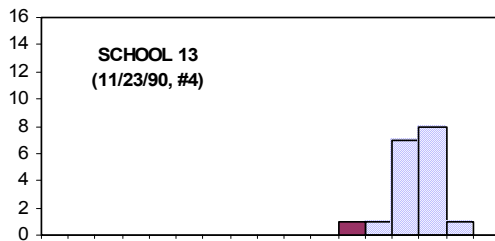
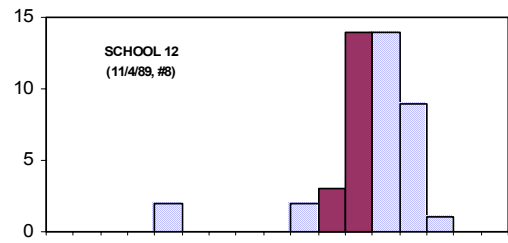
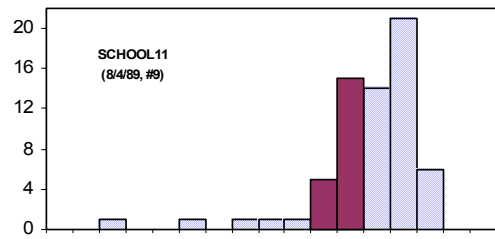
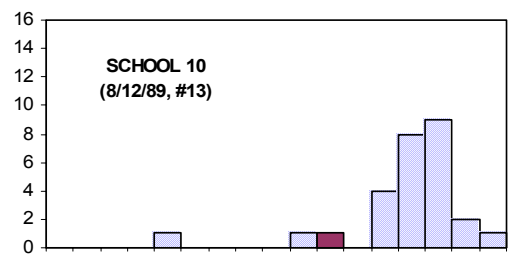
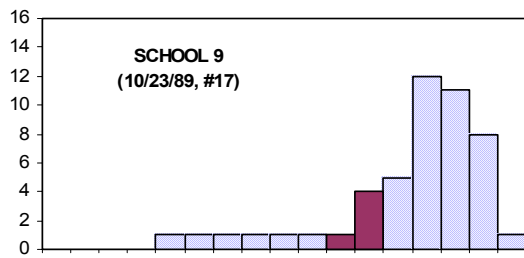
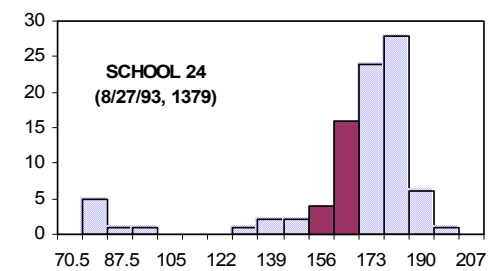
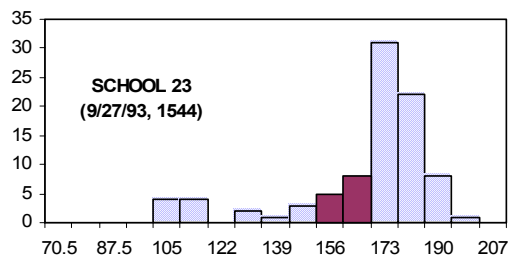
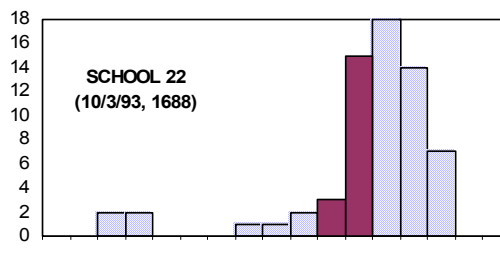
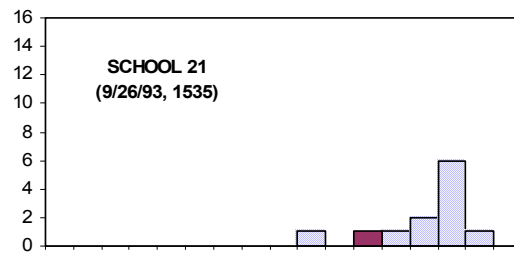
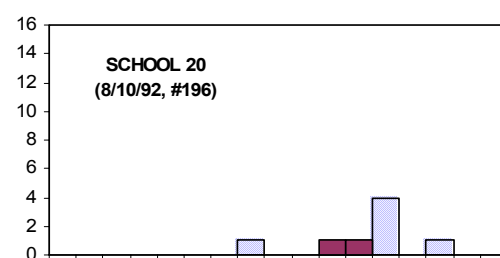
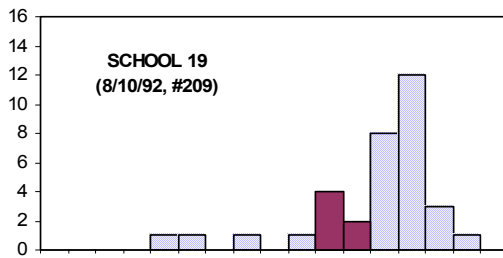
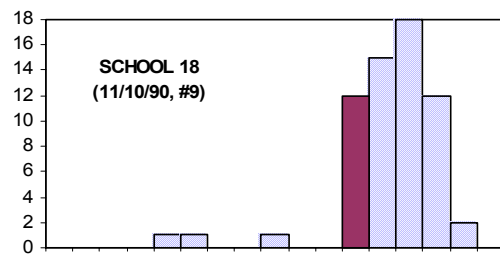
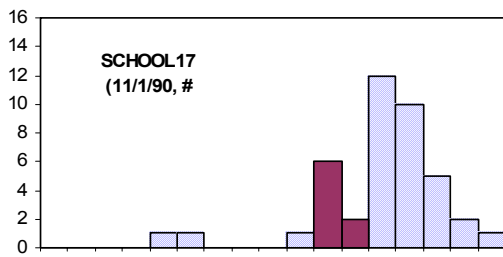


Figure 7. (continued)



length (cm)

length (cm)

Figure 7. (continued)

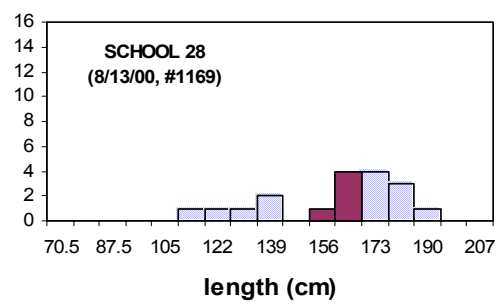
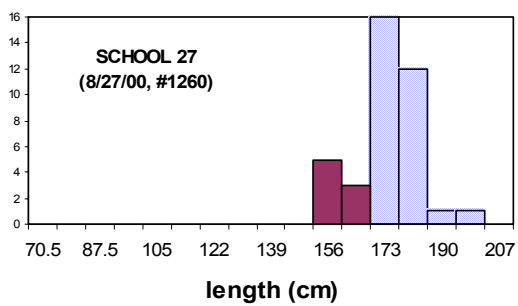
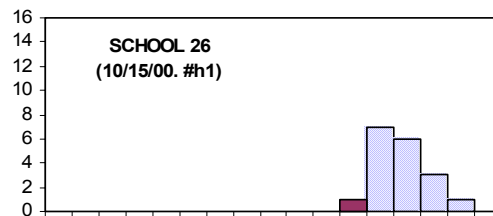
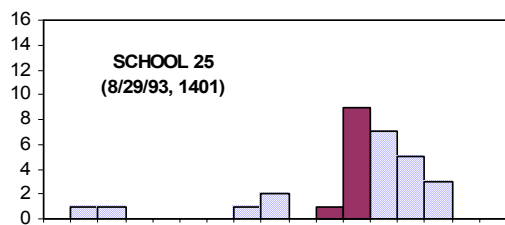


Figure 7. (continued)

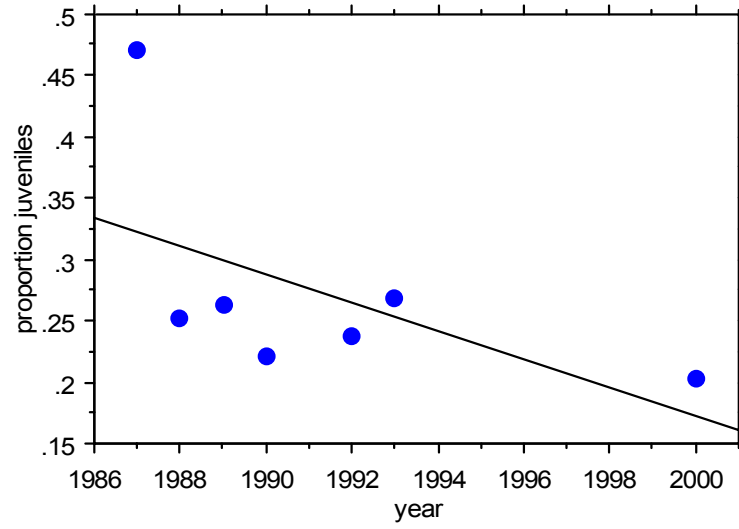


Figure 8. Proportion of animals in the juvenile length category versus year in which school was photographed. Data from schools within the same year are pooled.

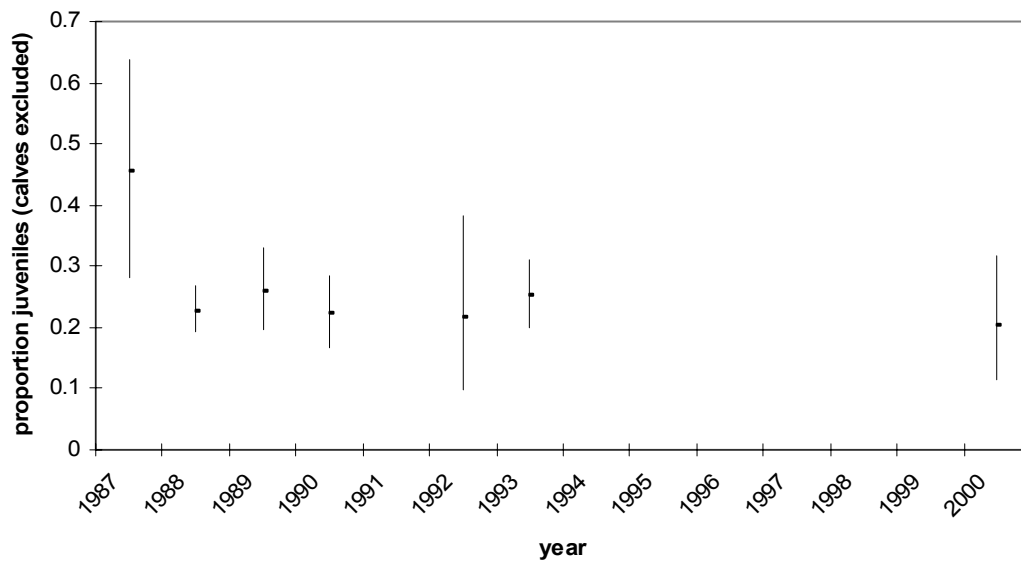


Figure 9. Proportion juveniles from data pooled within year with 95% binomial confidence intervals.

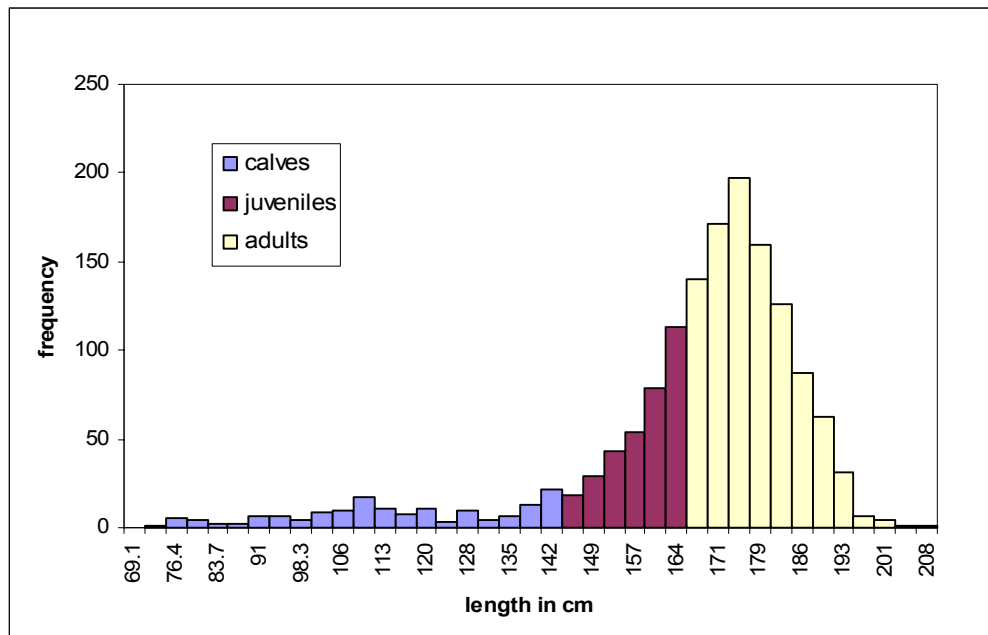


Figure 10. Length frequency distribution of all eastern spinner dolphins measured from photographic data. Lengths are stratified into three age classes: calf (≤ 147 cm), juvenile (147-164 cm), and adult (> 164 cm).

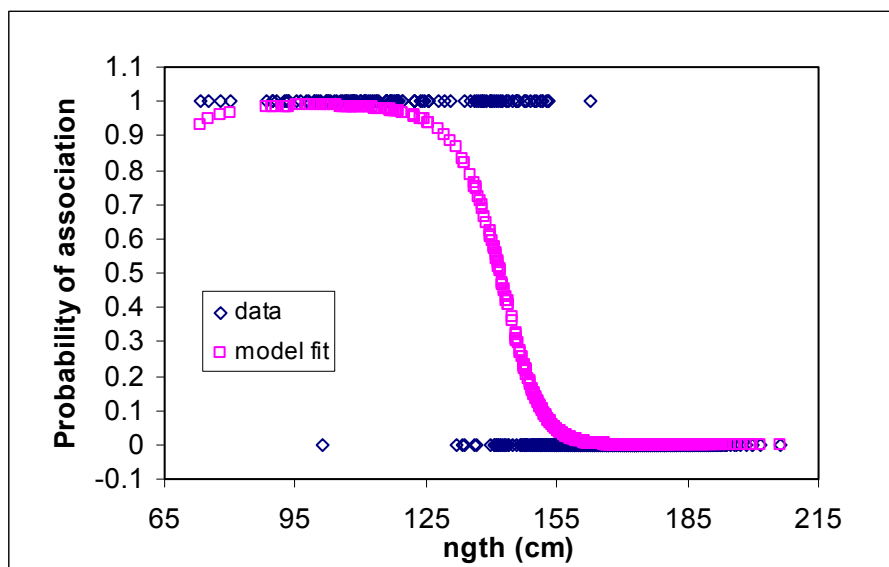


Figure 11. Probability of association with a cow as a function of body length. Open diamonds indicate association status of animal based on observed swimming configuration, open squares indicate probability of association as predicted by logistic regression model. ($n = 1199$)

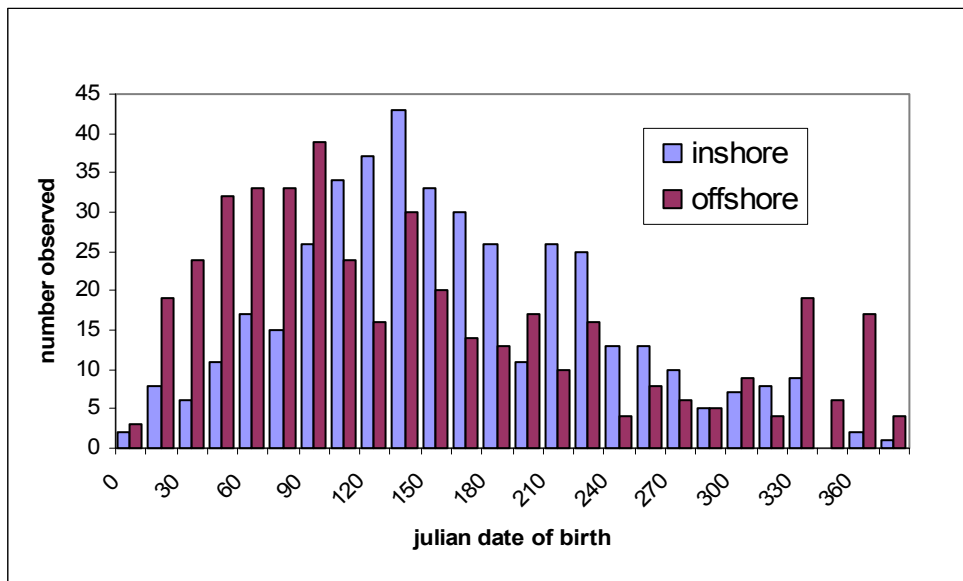


Figure 12. Frequency distribution of birthdates for eastern spinner yearlings from photograph and kill specimen data stratified by inshore and offshore regions.

APPENDIX A

Responses to CIE Reviewer Comments

DeGuise

"The conclusions seemed to be based on scarce data points irregularly spaced in time, and sometimes without taking into account some data points that do not fit the conclusions reached (in particular, with reference to Figure 6)" [which is Figure 5 in the present draft].

Response: The photographic data used in these analyses were collected during ship-based marine mammal abundance cruises that were not conducted at regular time intervals. However, for the years in which data are available there are an adequate number of schools photographed from which to compare the estimates of population demographic parameters among years. The analysis comparing the pooled proportion of calves among years by observing the overlap in their confidence intervals takes all data points into account, but only those which were found to have significantly different values relative to other points are reported in the results section. An additional chi-square analysis has been conducted to compare the same parameter, and a similar pattern was found in which the proportion of calves estimated for the most recent data point (2000) was significantly lower than that estimated for points from the early 1990s.

"Proportions of juveniles might be more demographically relevant than the proportion of calves " for the determination of the behavior of population dynamics.

Response: This is a good suggestion - a change in the proportion of juvenile animals may be a more reliable tool to assess population recovery than the proportion of calves, and the process of sampling juveniles in the photographs may be subject to less bias than that for calves. Unfortunately, the measurement data required to obtain the proportion of juvenile animals are much more scarce than the count data required to obtain the proportion of calves. Efforts can be made in the future to focus more on obtaining this type of data.

The paper examines patterns in the proportion of juveniles among schools and among years. We investigated possible patterns in the proportion of juveniles over time by performing a linear regression and by comparing the overlap in confidence intervals among years. Although there are fewer data points available for inspection than that for the proportion of calves, a similar downward pattern is apparent between the proportion of juveniles in the most recent years sampled versus those sampled earlier in the time series.

Mann

"Revised estimates of population growth and recovery for *Stenella* should be generated using estimates of 2-3 year calving intervals."

Response: This is a useful suggestion, and we intend to incorporate the estimate of age at disassociation obtained in this paper in a population model for this species in the future. The assessment model of the population dynamics of this species, currently in progress, incorporates this information.

"The two year weaning date might still be an underestimate if, as stated, the population is well below its carrying capacity."

Response: We have attempted in the past to stratify the data in order to estimate a separate length at disassociation for different periods across the time series; unfortunately, there are not enough length data from recent years to obtain a reliable estimate for the data collected after 1993. Effort should be made to obtain more photographic length data during future surveys to determine if the time at weaning is shifting in response to changing population levels.

"...the resolution of the photographs may allow closer analysis of possible "misses" in calf counts."

Response: All animals in the photographs were analyzed under the highest resolution possible. Any pairs of animals whose status as a cow/calf pair or non-cow/calf pair could not be determined initially were scrutinized to the best of our abilities until either, a) a positive determination could be made, or b) the animals were excluded from the data.

Bossart and Martineau

No specific recommendations were made by these reviewers.